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Seasonal, inter-annual and decadal drivers of tree and grass productivity in an Australian tropical savanna.

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Keywords:	MODIS, Gross Primary Productivity, DIFFUSE model, random forest, carbon sequestration, southern oscillation index
Abstract:	Tree-grass savannas are a widespread biome and are highly valued for their ecosystem services. There is a need to understand the long-term dynamics and meteorological drivers of both tree and grass productivity separately in order to successfully manage savannas in the future. This study investigated the inter-annual variability (IAV) of tree and grass gross primary productivity (GPP) by combining a long-term (15 year) eddy covariance flux record and model estimates of tree and grass GPP inferred from satellite remote sensing. On a seasonal basis, the primary drivers of tree and grass GPP were solar radiation in the wet season and soil moisture in the dry season. On an inter-annual basis, soil water availability had a positive effect on tree GPP and a negative effect on grass GPP. No linear trend in the tree-grass GPP ratio was observed over the 15 year study period. However, the tree-grass GPP ratio was correlated with modes of climate variability, namely the Southern Oscillation Index. This study has provided insight into the long-term contributions of trees and grasses to savanna productivity, along with their respective meteorological determinants of IAV.



For Review Only

1 **Title**

2 Seasonal, inter-annual and decadal drivers of tree and grass productivity in an Australian
3 tropical savanna.

5 **Running Head**

6 Savanna tree and grass productivity

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Abstract

Tree-grass savannas are a widespread biome and are highly valued for their ecosystem services. There is a need to understand the long-term dynamics and meteorological drivers of both tree and grass productivity separately in order to successfully manage savannas in the future. This study investigated the inter-annual variability (IAV) of tree and grass gross primary productivity (GPP) by combining a long-term (15 year) eddy covariance flux record and model estimates of tree and grass GPP inferred from satellite remote sensing. On a seasonal basis, the primary drivers of tree and grass GPP were solar radiation in the wet season and soil moisture in the dry season. On an inter-annual basis, soil water availability had a positive effect on tree GPP and a negative effect on grass GPP. No linear trend in the tree-grass GPP ratio was observed over the 15 year study period. However, the tree-grass GPP ratio was correlated with modes of climate variability, namely the Southern Oscillation Index. This study has provided insight into the long-term contributions of trees and grasses to savanna productivity, along with their respective meteorological determinants of IAV.

49 **Introduction**

50 Savannas are a widespread biome characterised by a coexistence of trees and grasses that
51 cover approximately 20 % of the global land surface (Scholes & Archer, 1997). They inhabit
52 the continents of Australia, Africa, the Americas, Europe and Asia and are a vital source of
53 food, timber products and income for a quarter of the world's human population (Mistry,
54 2001; Scholes & Archer, 1997; Shackleton et al., 2002). Savannas are also a key biome for
55 terrestrial atmospheric carbon uptake via gross primary productivity (GPP), accounting for
56 some 25 % of global GPP each year (Beer et al., 2010; Grace, José, Meir, Miranda, & Montes,
57 2006). However, plant respiration consumes approximately half of GPP, while heterotrophic
58 respiration contributes to further carbon release to the atmosphere (Bonan, 2008; Chapin III,
59 Matson, & Vitousek, 2011). Over longer timescales, disturbances such as grazing, land cover
60 change (Bristow et al., 2016; Hutley et al., 2013; Hutley & Beringer, 2010), and fire
61 (Beringer et al., 2015; Bond & Keeley, 2005; Bowman et al., 2010; Shi, Matsunaga, Saito,
62 Yamaguchi, & Chen, 2015; Van Der Werf et al., 2010) return a portion of the sequestered
63 carbon from GPP back to the atmosphere. Taking these factors into account, savanna
64 ecosystems are still an important terrestrial sink of atmospheric carbon ($0.5 - 2.0 \text{ Gt C y}^{-1}$
65 globally; Grace, José, Meir, Miranda, & Montes, (2006); Scurlock & Hall, (1998)) and
66 explain a large portion of inter-annual variability in the global land carbon sink (Ahlström et
67 al., 2015; Poulter et al., 2014). Nevertheless, the seasonal, annual and inter-annual
68 partitioning of this productivity between trees and grasses is still poorly understood for
69 savannas (Moore et al., 2016; Whitley et al., 2011), which limits our ability to make informed
70 decisions about savanna management into the future (Dyer & Smith, 2003; Scheiter, Higgins,
71 Beringer, & Hutley, 2015; Shackleton et al., 2002; Walsh, Russell-Smith, & Cowley, 2014).

72 As the climate changes into the 21st century, there is uncertainty about how savanna
73 ecosystems will respond (Scheiter & Higgins, 2009; Scheiter et al., 2015). Global climate

74 projections anticipate an increase in temperature and rainfall amount for most savanna
75 regions as atmospheric carbon dioxide (CO₂) continues to rise (van Oldenborgh et al., 2013).
76 Such changes to rainfall regimes will directly affect savannas due to the pivotal role of
77 moisture availability as a driver of productivity (Beringer et al., 2011; Kanniah, Beringer, &
78 Hutley, 2010, 2011; Whitley et al., 2011). Rising CO₂ poses an additional threat to savanna
79 ecosystems from the effects of carbon fertilisation on savanna tree-grass structure. Tropical
80 savanna grasses use a different photosynthetic pathway (C₄) when compared to the trees (C₃),
81 which concentrates CO₂ at the photosynthetic reaction centres and provides grasses with a
82 photosynthetic advantage over trees under current atmospheric conditions (Beerling &
83 Osborne, 2006; Sage, 2004). Under higher atmospheric CO₂ tree productivity will be less
84 limited by CO₂ availability, so they may experience a competitive advantage over the grasses
85 as a result (Higgins & Scheiter, 2012). This phenomenon, where trees outcompete grasses,
86 has been termed woody thickening, which is defined for savannas as an increase in woody
87 standing biomass (Macinnis-Ng, Zeppel, Williams, & Eamus, 2011) and is likely to
88 accelerate in coming decades (Browning, Archer, Asner, McClaran, & Wessman, 2008; Field,
89 Lobell, Peters, & Chiariello, 2007; Scheiter & Higgins, 2009; Scheiter et al., 2015).
90 Evergreen vegetation that persists year round will receive the greatest advantage from this
91 CO₂ fertilisation effect (Donohue, McVicar, & Roderick, 2009), particularly in seasonally
92 water limited and arid environments (Donohue, Roderick, McVicar, & Farquhar, 2013).
93 Dynamic vegetation modelling in African (Scheiter & Higgins, 2009) and Australian
94 (Scheiter et al., 2015) savannas has attributed increased atmospheric CO₂ and fire suppression
95 as the primary drivers of this woody thickening.

96 To determine how woody thickening might change savanna tree-grass dynamics in the future,
97 we need an understanding of how the trees and grasses have interacted in the past. We know
98 that tree productivity declines from the wet to dry season in response to declining plant

99 available moisture and the resultant reduction in leaf area (Cernusak, Hutley, Beringer,
100 Holtum, & Turner, 2011; Eamus, Hutley, & O'Grady, 2001; Eamus, Myers, Duff, &
101 Williams, 1999; Eamus & Prior, 2001). Fire is also an important regulator of both ecosystem
102 productivity (Beringer et al., 2003; Beringer et al., 2015; Beringer, Hutley, Tapper, &
103 Cernusak, 2007) and the biomass proportion of trees to grasses. Fire is fuelled by dead grassy
104 biomass and suppresses juvenile woody recruitment to the overstory (Murphy, Russell-Smith,
105 & Prior, 2010; Prior et al., 2006; Werner & Prior, 2013). Over longer timescales, macro-scale
106 cyclical climate modes such as El Niño/La Niña, monsoonal systems and cyclones influence
107 the amount of rainfall received in savanna regions (Hutley et al., 2013; Rogers & Beringer,
108 2017), which in turn has an effect on the productivity and tree-grass biomass of savanna
109 ecosystems. Recent work from Moore et al., (2016) presents one of the first attempts at
110 quantifying the relative contributions of productivity between trees and grasses using the
111 eddy covariance technique. This study showed that in an Australian savanna, productivity
112 was driven by both a strong seasonal input from the grasses and a comparatively consistent
113 input from the trees. A model-based study at the same site as used by Moore et al., (2016),
114 showed the importance of light limitation on tree-grass productivity (Whitley et al., 2011).
115 While these two studies demonstrated the interaction of trees and grasses within the savanna
116 ecosystem, both identified the need for longer term studies to explore the productivity
117 dynamics of trees and grasses in more detail. In support of this, recent work from Ma,
118 Baldocchi, Wolf, & Verfaillie, (2016) indicated that an ecosystem's carbon balance can
119 respond slowly to climatological forcing, highlighting the need for more long term studies
120 that explore such dynamics.

121 The combination of *in situ* monitoring and satellite remote sensing provides the tools
122 necessary for establishing long term research studies that explore productivity dynamics
123 within savanna ecosystems. In recent years, techniques have been developed using satellite

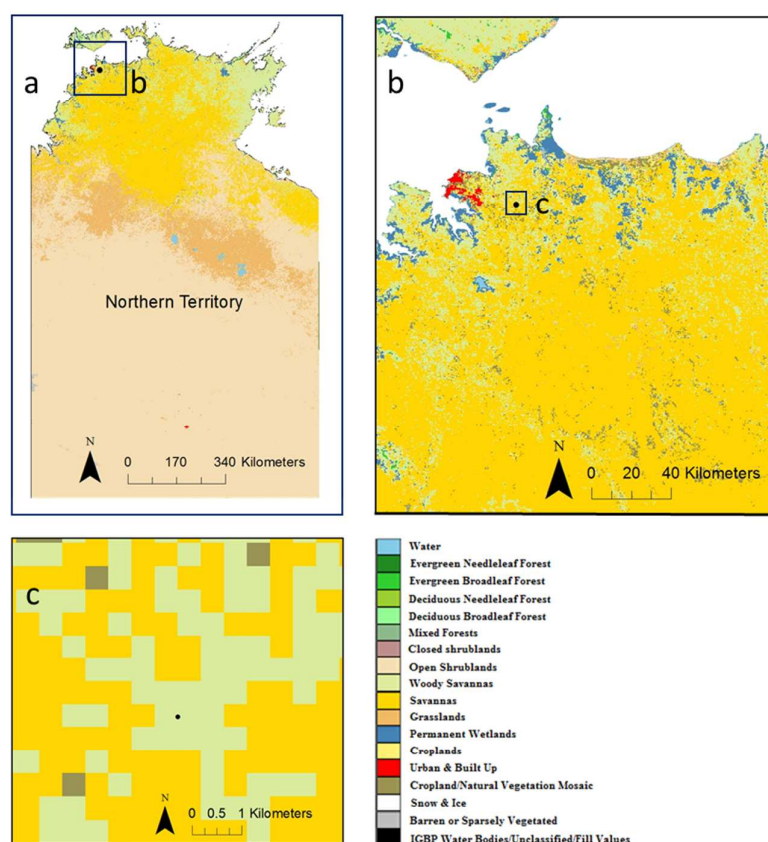
data to isolate tree and grass fractions in mixed ecosystems (Donohue et al., 2014; Zhou, Hill, Sun, & Schaaf, 2016); with time-series available from 2001 (i.e. MODerate resolution Imaging Spectroradiometer (MODIS)). Additionally, ecosystem monitoring at the Howard Springs savanna research site in Australia began in 1997 (Eamus, Hutley, & O'Grady, 2001) and the site now forms part of the Australian and New Zealand flux network (OzFlux), with continuous monitoring of fluxes since 2001 (Beringer et al., 2016). The continuous flux dataset, coupled with MODIS data, provides 15 years of information to explore the magnitude and underlying meteorological variables responsible for inter-annual variability in tree and grass productivity. Using this 15-year data set, we addressed the following research questions; (i) what are the most important meteorological factors that govern long-term productivity dynamics of trees and grasses in this savanna?; (ii) Is there any link between macro-scale climate modes and tree-grass GPP at our site?; and (iii) Can we detect woody thickening at our site? Understanding the importance of climatological factors for savanna tree-grass structure and productivity will contribute towards improvement of predictions of the impacts of climate change on this key global ecosystem.

Methods

Study site

The Howard Springs OzFlux and Fluxnet (AU-How) research site was used for this study, which is a mesic tropical savanna in the Northern Territory, Australia. Howard Springs (Fig. 1; c), and the wider Northern Territory region (Fig. 1; a & b), is classified as mixed 'savanna' and 'woody savanna' by the MODIS land cover product (MCD12Q1) that uses the International Geosphere-Biosphere Program (IGBP) defined land cover types (Friedl et al., 2002). The tree overstory comprises mostly *Eucalyptus miniata* and *E. tetrodonta*, with lesser abundant semi-, brevi- and fully deciduous species throughout, including *Terminalia*

ferdinandiana and *Erythrophleum chlorostachys* (Hutley, Beringer, Isaac, Hacker, & Cernusak, 2011; Williams, Myers, Muller, Duff, & Eamus, 1997). The understory consists mostly of C₄ grasses, including the annual *Sorghum intrans* and the perennials *Heteropogon triticeous* and *S. plumosum*, but also woody species including *Cycas armstrongii* and juvenile overstory species (Moore et al., 2016). The rainy season months from mid-October to mid-April account for 90-95 % of Howard Springs' mean annual rainfall of 1732 (\pm 44 SE, from 1941-2014) mm, (Australian Bureau of Meteorology (BoM), station ID: 014015, www.bom.gov.au). Mean daily air temperature (from 1941-2014) is very consistent throughout the year, with the monthly maxima ranging between 30.6 and 33.3 °C and minima between 19.3 and 25.3 °C (BoM, station ID: 014015, www.bom.gov.au). Soils in the region are weathered and nutrient poor red Kandosols (Isbell, 1996). Fire frequently occurs across the region, with recurrence rates between 1-5 years (Beringer et al., 2015; Jeremy Russell-Smith & Yates, 2007) and on longer timescales, cyclone activity also causes large disturbance (Hutley et al., 2013; Hutley & Beringer, 2010).



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Figure 1: MODIS Land Cover Product (MCD12Q1) using the International Geosphere-Biosphere Program (IGBP) classification system for a) the Northern Territory in Australia, b) the northern-west region of the northern territory and c) the area directly surrounding the Howard Springs OzFlux tower, with individual pixel resolution of 500 m (produced in ArcMap v10.1 using MODIS Land Cover data from (Gibson, 2015).

Gross primary productivity from flux towers

Eddy covariance flux towers were used in this study to estimate total ecosystem GPP, and its overstory (tree) and understory (mostly grass) components, from measurements of net ecosystem exchange (NEE). A flux tower at Howard Springs has been in continuous operation since 2001 (Beringer et al., 2016; Eamus, Hutley, & O’Grady, 2001). In September 2012, an understory flux tower was installed to measure understory fluxes in conjunction with the ecosystem tower (Moore et al., 2016). The understory tower was installed 10 m to the west of the main ecosystem tower and recorded a representative footprint of the understory fluxes within that of the main tower. This arrangement of total ecosystem and understory measurements allowed for the separation of the overstory and understory carbon fluxes. The understory tower has been extensively validated by Moore et al., (2016), where details regarding the processing, quality assurance and quality control (QA/QC) of the flux data, as well as the partitioning of net ecosystem exchange (NEE) into respiration and GPP, and estimates of flux uncertainty can be found.

In brief, the principal eddy covariance instruments used in this study were an infrared gas analyser (LI-7500, LI-COR Biosciences, Lincoln, NE) and a three dimensional sonic anemometer (CSAT3, Campbell Scientific, Logan, UT). Both instruments measured at a rate of 10 Hz and were averaged to 30-minute covariances of vertical wind velocity and scalars of carbon, water and heat between the land surface and the atmosphere. In addition, measurements of soil heat flux (HFT3, Campbell Scientific, Logan, UT), temperature (TCAV, Campbell Scientific, Logan, UT) and moisture content (CS616, Campbell Scientific, Logan, UT) were made along with net/short/long wave radiation (CNR4, Kipp and Zonen, Delft, NL), air temperature and humidity (HMP45A, Vaisala, Vantaa, FI) and precipitation (TB3, Hydrological Services, NSW, AU) on 30-minute averages.

The raw flux data were QA/QC'd to level 3 (L3) using the OzFluxQC (v2.9.4) standard processing scripts (Isaac et al., 2017). Energy balance closure for the ecosystem tower 0.89 with an r^2 of 0.92 determined for daily data as per Leuning, van Gorsel, Massman, & Isaac, (2012). We did not calculate energy balance closure for the understory tower due to the difficulty in obtaining an accurate net radiation estimate. Instead, a co-spectral analysis was performed on 10 Hz understory data to ensure the tower recorded turbulent fluxes during the day (Moore et al., 2016). To gap fill the L3 flux data and partition NEE into respiration and GPP, the Dynamic Integrated Gap filling and partitioning for OzFlux (DINGO) was used (Beringer, Mchugh, Hutley, Isaac, & Kljun, 2017). This process was performed on 3 years of understory data (2012-2015) and 15 years of ecosystem data (2001-2015). Once NEE was gap-filled, model and random error was calculated based on McHugh et al. (2017), revealing an error of $21.2 \text{ g C m}^{-2} \text{ y}^{-1}$ (4 % of NEE) for ecosystem and $25.8 \text{ g C m}^{-2} \text{ y}^{-1}$ (3.5 % of NEE) for understory (Moore et al., 2016).

218 *Modelling tree and grass GPP*

219 To provide an estimate of tree and grass GPP over the past 15 years, we used the DIFFUSE
220 model described by Donohue et al., (2014), which evaluates the fraction of tree and grass
221 components based on their absorption of photosynthetically active radiation (PAR). The
222 DIFFUSE model is formulated on the basis of Monteith's (1972) light use efficiency (LUE)
223 model, estimating photosynthesis as a product of light absorbed (i.e. fraction of absorbed
224 photosynthetically active radiation; APAR) along with the efficiency of its use (LUE,
225 Equation 1):

226
$$GPP = C \times Fsd \times fPAR \times LUE$$
 Equation 1

227 where fPAR refers to the fraction of PAR absorbed by an ecosystem, Fsd is shortwave
228 radiation ($J\ m^{-2}\ d^{-1}$) and C is a constant that converts shortwave radiation into PAR ($C \approx 2.3 \times$
229 $10^{-6}\ mol\ J^{-1}$). fPAR was calculated from the MODIS normalised difference vegetation index
230 (NDVI) product (MOD13Q1) following Donohue et al., (2014). Fsd was calculated using
231 meteorological grids of radiation at 0.05° resolution (downscaled to 250 m) and shuttle radar
232 topographic mission (SRTM) elevation data at 1 s resolution to account for the effects of
233 topography on Fsd. Donohue, McVicar, & Roderick, (2010) provide a detailed explanation of
234 Fsd calculation. The DIFFUSE model estimates LUE as a function of maximum
235 photosynthesis under direct radiation (i.e. A_x) and the diffuse (D_f) fraction of total incoming
236 radiation. D_f varies depending on sky conditions from 1.0 under a fully overcast sky to 0.2
237 under clear sky conditions (Roderick, 1999). Taking this into account, the DIFFUSE model
238 estimates LUE as (Equation 2):

239
$$LUE = 0.024D_f + 0.00061A_x$$
 Equation

where A_x is the maximum rate of photosynthesis at the top of a canopy ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and the two constants (0.024 is unitless, 0.0061 has units of $\mu\text{mol PAR m}^{-2} \text{ s}^{-1}$) are calculated from empirical observations of solar radiation across Australia (Roderick, 1999). The DIFFUSE model was parametrised at the continental scale for Australia using satellite remote sensing data (primarily from MODIS) and was validated against 12 OzFlux monitoring sites (Donohue et al., 2014). Equations 1 and 2 form the basis of the DIFFUSE model that provides data output in monthly resolution. Further information about DIFFUSE can be found in Donohue et al., (2014).

It should be noted that there may be some small differences between DIFFUSE and flux tower estimates because DIFFUSE evaluates the grass (and tree) components, whereas the flux tower measures the understory (grass plus some small shrubs). We have previously shown that in the savanna understory, grasses are the dominant vegetation during the wet season, with fire-suppressed saplings of the dominant woody tree and shrub species accounting for a modest fraction (~18 %) of annual GPP (Moore et al., 2016;, 2017). This contribution is particularly evident in the dry season when the senesced grasses do not contribute to GPP (Moore et al., 2016, 2017). The flux tower GPP estimates from the understory include this juvenile woody component, whereas the DIFFUSE model estimates were of C_3 (i.e. tree) and C_4 (i.e. grass) contributions. In addition, DIFFUSE was calculated from MODIS indices, whose temporal resolution is coarser than that of the flux towers. Therefore, we do not expect them to completely agree. From herein, we use tree and grass GPP to refer to the DIFFUSE model estimates and overstory and understory to refer to the flux tower estimates.

Despite the model-flux tower differences, the DIFFUSE grass estimates did capture the seasonality of the flux tower understory quite well, except that in preliminary simulations a model lag existed during the transition from wet to dry season (i.e. March to May). We

266 suspected this was due to the phenology of the C₄ annual grasses that dominate understory
267 biomass not being fully captured by the DIFFUSE model. However, if it is assumed that the
268 foliage cover of evergreen (or perennial) vegetation is reasonably invariant across seasons
269 and that of annual (and ephemeral) vegetation is highly variable, the contribution of these two
270 components to total foliage cover can be approximated. Donohue, McVicar, & Roderick
271 (2009) developed such a method using a moving minimum approach. Due to the almost
272 complete absence of deciduous vegetation in Australia, this approach has been shown to
273 provide a reliable estimate of tree and grass foliage cover (Gill, Armston, Phinn, & Pailthorpe,
274 2006). Here, instead of applying this splitting method to foliage cover and using tree and
275 grass cover to produce separate DIFFUSE-based estimates of tree and grass, we calculated
276 ecosystem GPP using the DIFFUSE model and then applied the Donohue, McVicar, &
277 Roderick, (2009) splitting algorithm to produce tree and grass GPP. This approach improved
278 the ability of the DIFFUSE model to capture the seasonal dynamics of the understory flux
279 tower (Figure 2) and these results are used in the following analyses. Tree GPP was then
280 calculated as the difference between flux tower ecosystem GPP and DIFFUSE grass GPP as
281 (Equation 3):

282
$$GPP_{Tree} = GPP_{Eco} - GPP_{Grass}$$
 Equation
283 3

284 where GPP_{Eco} is the flux tower ecosystem GPP estimate and GPP_{Grass} is the DIFFUSE model
285 GPP estimate. This method provided the closest fit with tree GPP estimates from the flux
286 tower.

287

288 *Determining the drivers of tree and grass productivity*

289 Savanna ecosystem GPP varies over distinct time scales in response to meteorological and
290 climatological conditions (Beringer et al., 2011; Kanniah, Beringer, & Hutley, 2010). Once
291 we separated long-term ecosystem GPP into tree and grass estimates, we calculated anomaly
292 values based on data grouped by water-year (i.e. July-June), to ensure the anomalies
293 represented complete growing seasons. Tree and grass GPP anomalies, calculated as a change
294 in yearly GPP ($\text{g C m}^{-2} \text{ y}^{-1}$) from the 14 water-year mean, were compared against anomaly
295 values using linear regressions for six primary meteorological drivers that are known to
296 influence GPP (Kanniah et al., 2010). These drivers were also measured by the flux tower,
297 and included solar radiation (Fsd, $\text{MJ m}^{-2} \text{ y}^{-1}$), precipitation (Precip, mm y^{-1}), air temperature
298 (T_a , $^{\circ}\text{C}$), vapour pressure deficit (VPD, kPa), soil water storage (Sws, $\text{m}^3 \text{ m}^{-3} \text{ y}^{-1}$) and rainy
299 season length (RS, number of days per year).

300 To explore seasonality in the meteorological drivers of tree and grass GPP for each month of
301 the year, we used the Random Forest machine learning technique described by Breiman,
302 (2001), and implemented using the Python Scikit-Learn module (Pedregosa et al., 2011). The
303 Random Forest merges multiple mathematical decision trees ($n = 1000$) to split a population
304 of dependent variables (i.e. GPP) as a function of a number of independent variables (i.e.
305 meteorology). Each input variable was allocated an 'importance' value that was based on a
306 tree-wise comparison of the explanatory power of the variables of each tree. Relative
307 importance ranges from 0 – 1, with 0 indicating no importance and 1 indicating sole
308 importance (Breiman, 2001; Exbrayat & Williams, 2015; López-Blanco et al., 2017). We
309 tested the meteorological variables of Fsd, Precip, T_a , VPD and Sws on daily averaged data
310 from 2001 to 2015 using Random Forests, and then grouped this data by month to investigate
311 seasonal variability and IAV. Initial analysis used soil moisture at 10 cm, as this was
312 available throughout the entire 15-year record. This surface Sws at 10 cm is quickly reduced

below field capacity in the dry season (Duff et al., 1997; Moore et al., 2016; Walker & Langridge, 1997). To test the relative importance of deeper Sws for productivity, we added a 100 cm Sws measurement over a reduced time period (2008 to 2015), to account for installation of the 100 cm sensor at the beginning of 2008. Given the shorter temporal length of the 100 cm Sws time series, we did not use it in our IAV analysis.

Lastly, to explore long-term trends in the productivity of the trees and grasses, we calculated a simple tree-grass GPP ratio (i.e. tree/grass) and plotted its annual anomaly values. Changes in the tree-grass GPP ratio and anomaly values over time can provide an indication of the potential for woody thickening at the site over the last 15 years. The anomaly values were also compared against four key climate indices of climate variability that have been found to perform well at describing long-term annual rainfall patterns at the Howard Springs site (Rogers & Beringer, 2017). These four indices were the Southern Oscillation Index (SOI), the Tasman Sea Index (TSI), the Indonesia Index (II) and the Australian Monsoon Index (AUSMI). The SOI is a measure of the monthly mean sea level pressure difference between Darwin and Tahiti and is commonly used as an indicator of El Niño and La Niña events (Nicholls, 1991; Nicholls, 1989; Suppiah & Hennessy, 1996). The TSI and II are calculated from sea surface temperatures, with the TSI from a region off the east coast of Australia (150 °E to 160 °E and 40 °S to 30 °S, (Murphy & Timbal, 2008)) and the II from a region surrounding Indonesia (120 °E to 130 °E and 0 °N to 10 °S, (Nicholls, 1989; Schepen, Wang, & Robertson, 2012)). The AUSMI provides an indication of the occurrence of the summer monsoon that is a primary mechanism for delivering rainfall in northern Australia (Sturman & Tapper, 2006). It is calculated from zonal wind velocity at 850 mb over a region of Indonesia and north western Australia (110 °E to 130 °E and 5 °S to 15 °S, (Kajikawa, Wang, & Yang, 2010)). Annual (i.e. water-year) anomaly values were calculated for each index based on daily (TSI and II), monthly (SOI), or seasonal (AUSMI) data availability, which

were regressed against the annual tree-grass anomaly values to assess their correlations. Correlations were expressed as significant based on p-values <0.05 .

Results

Long-term tree and grass GPP dynamics

To partition long-term ecosystem GPP at Howard Springs into tree and grass contributions, we first validated DIFFUSE model estimates of GPP against flux tower estimates for the 15-year ecosystem record and for the three years the understory tower was in operation (2012–2015). The DIFFUSE model performed well at capturing ecosystem flux tower seasonality in GPP over the 15-year study period ($r^2 = 0.83$; Figure 2, a), as well as the shorter 3-year subset ($r^2 = 0.81$; Figure 2, b). DIFFUSE also captured the seasonality of the grasses well, but slightly underestimated understory GPP in the dry season ($r^2 = 0.82$; Fig. 2, c). In contrast to the grasses, DIFFUSE performed less well at capturing the timing of tree GPP ($r^2 = 0.39$; Fig. 2, d). Given the overall strong fit between DIFFUSE and flux tower ecosystem GPP estimates, plus the strong fit of DIFFUSE with understory flux tower GPP, we used the grass DIFFUSE model to predict grass productivity over the 15-year ecosystem flux time-series.

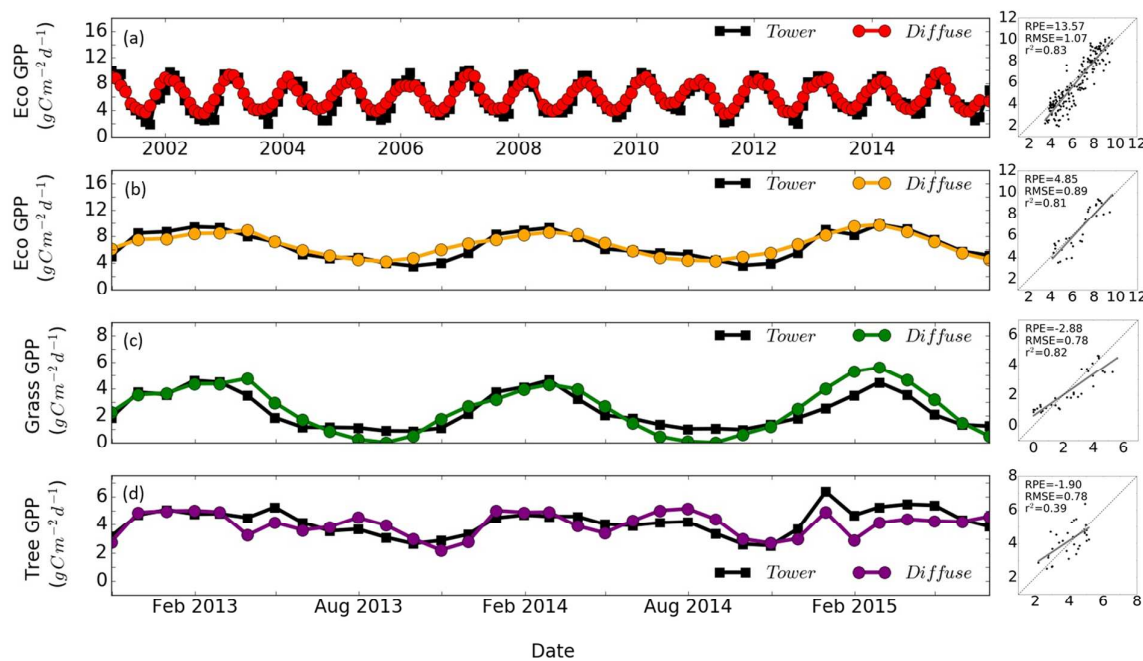


Figure 2: Time series and regression comparison of Howard Springs flux tower and DIFFUSE model estimates of gross primary productivity (GPP, $\text{g C m}^{-2} \text{d}^{-1}$) for (a) 15 years (2001-2015) of ecosystem fluxes, and 3 years (September 2012 to June 2015) of fluxes for (b) ecosystem, (c) grass and (d) tree. Regression plots show the line of best fit (solid line), the 1:1 line (dashed line), the relative predictive error (RPE, %), the root mean square error (RMSE, $\text{g C m}^{-2} \text{d}^{-1}$) and the r^2 fit.

Using the DIFFUSE model grass GPP fraction, we then partitioned the long-term ecosystem GPP tower estimate into monthly tree and grass contributions (Fig. 3). On an annual basis, the grasses contributed an average of 41 % to ecosystem GPP, with a range from as low as 33 % in some years (i.e. 2010) and up to 50 % in other years (i.e. 2002 to 2003 and 2015, Fig. 3).

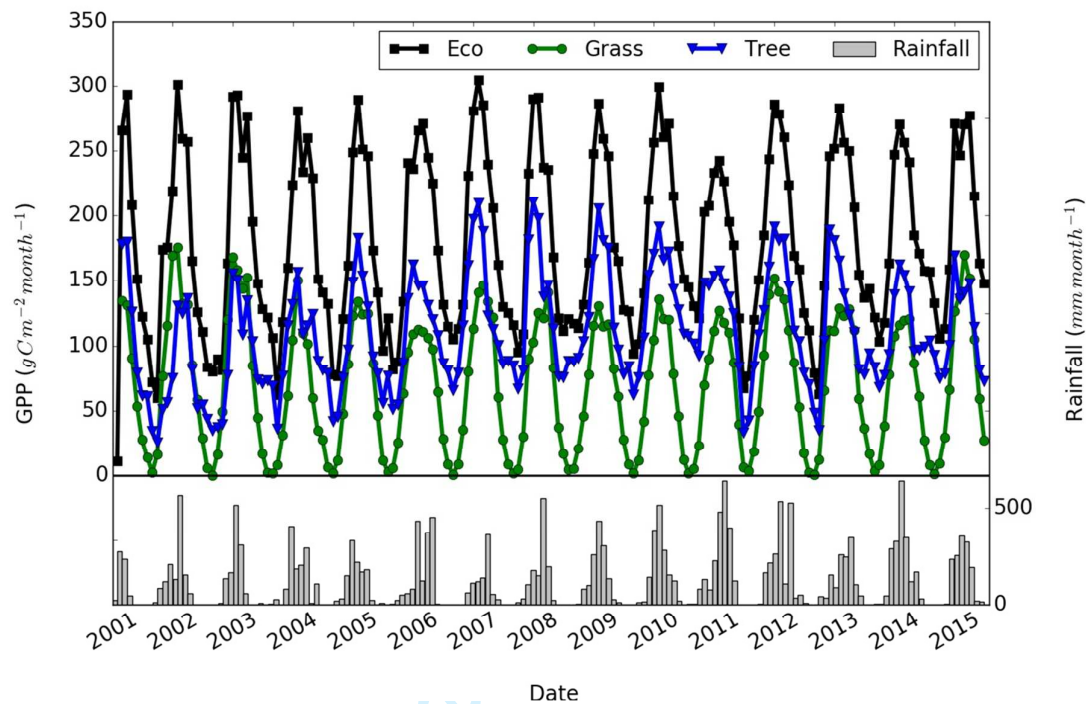
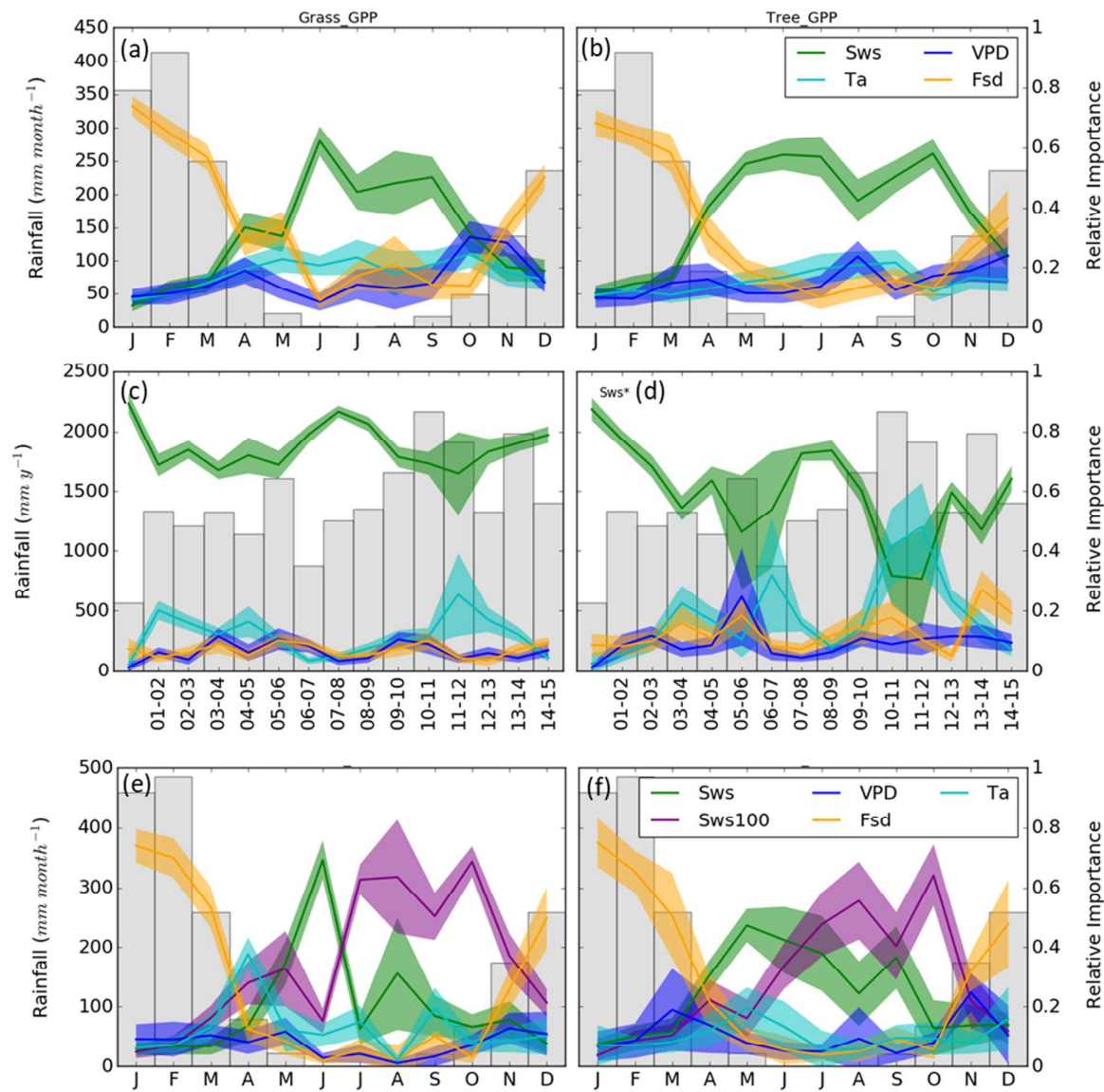


Figure 3: Long-term (15 year) ecosystem (Eco) gross primary productivity (GPP) flux tower time series, the partitioned (modelled) tree and grass GPP, plus rainfall, for the Howard Springs savanna site. Data are shown as monthly sums.

Seasonal and inter-annual drivers of tree and grass productivity

To analyse what meteorological variables are most important for seasonality of GPP, and if they differed between the trees and grasses, we used the Random Forest technique. This approach revealed that solar radiation (Fsd) was, not surprisingly, the most important (qualitative indication of co-variation) variable for determining wet season productivity for both the trees and grasses (Fig. 4; a & b). In contrast to the wet season, soil water availability (Sws) was the most important driver of tree and grass productivity in the dry season (Fig. 4; a & b). At the onset of the dry season (Apr-May), the upper soil layers have the highest importance for productivity, which switches to deeper soil moisture as the dry season

382 progresses (Fig. 4; e & f). This result is also reflected in the inter-annual analysis, showing
383 that overall, Sws was the most important determinant of tree and grass GPP over the 15-year
384 time series (Fig. 4; c & d).



385

386 **Figure 4:** Meteorological drivers of monthly (a & b) and yearly (c & d) grass and tree gross
387 primary productivity (GPP) from 2001 to 2015, plus a shorter temporal monthly time
388 series (e & f) of tree and grass GPP from 2008 to 2015 at Howard Springs.

389 Meteorological drivers include soil water storage at 10 cm (Sws), Sws at 100 cm

(Sws100), air temperature (T_a), vapour pressure deficit (VPD) and incoming solar radiation (Fsd). The bottom panel begins in 2008 due to the installation of the 100 cm Sws sensor in that year.

To explore IAV in tree and grass GPP, we calculated and plotted anomalies based on their respective 14 water-year (i.e. Jul-Jun) mean GPP values (Fig. 5). These plots showed that the GPP anomalies for trees appeared to increase over time, but that grass anomalies fluctuated around the mean. Included in Fig. 5 are anomalies for changes in the yearly sum of daily mean Fsd, T_a , Sws, soil temperature (T_s), and VPD, as well as changes in total annual rainfall. To determine which of these variables best described changes in tree and grass productivity inter-annually, we used a simple linear regression analysis. This approach showed that of the six variables, only Sws had a statistically significant influence on the IAV of the tree ($p = 0.003$) and grass ($p = 0.006$) GPP anomalies (Fig. 6), a finding also supported by the IAV Random Forest analysis (Fig. 4; c & d). Interestingly, the trees showed a positive correlation with increasing Sws (Fig. 6; e), while the grasses revealed a negative correlation with the increasing Sws anomalies (Fig. 6; k).

The key year that stands out in the anomalies of the 15-year monitoring period is 2010-2011, where the highest positive rainfall anomaly (Fig. 5; f) and greatest negative Fsd anomaly (Fig. 5; b) occurred. While the tree GPP anomaly was positive, it was not the highest recorded during this time period (Fig. 5; a), and the grass anomaly was negative, but not the most so (Fig. 5; e). Both tree and grass GPP anomalies became noticeably more positive in the year proceeding the 2010-2011 meteorological anomaly year (i.e. 2011-2012), while Fsd and rainfall were less variable than in 2010-2011 (Fig. 5 b & f).

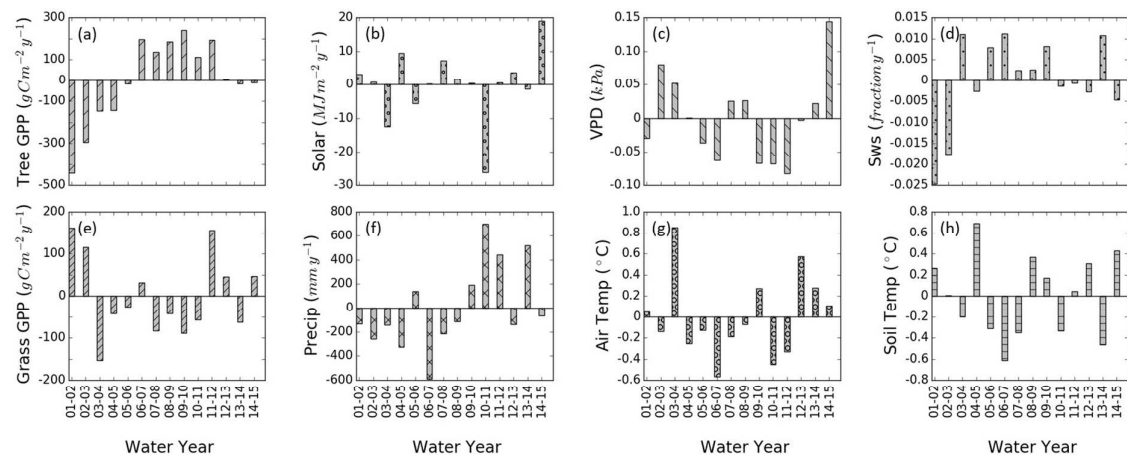


Figure 5: Anomaly plots for tree (a) and grass (e) GPP, plus solar radiation (Solar, b), vapour pressure deficit (VPD, c), soil water storage (Sws, d), rainfall (Precip, f) and air (Ta, g) and soil (Ts, h) temperature for the Howard Springs savanna site.

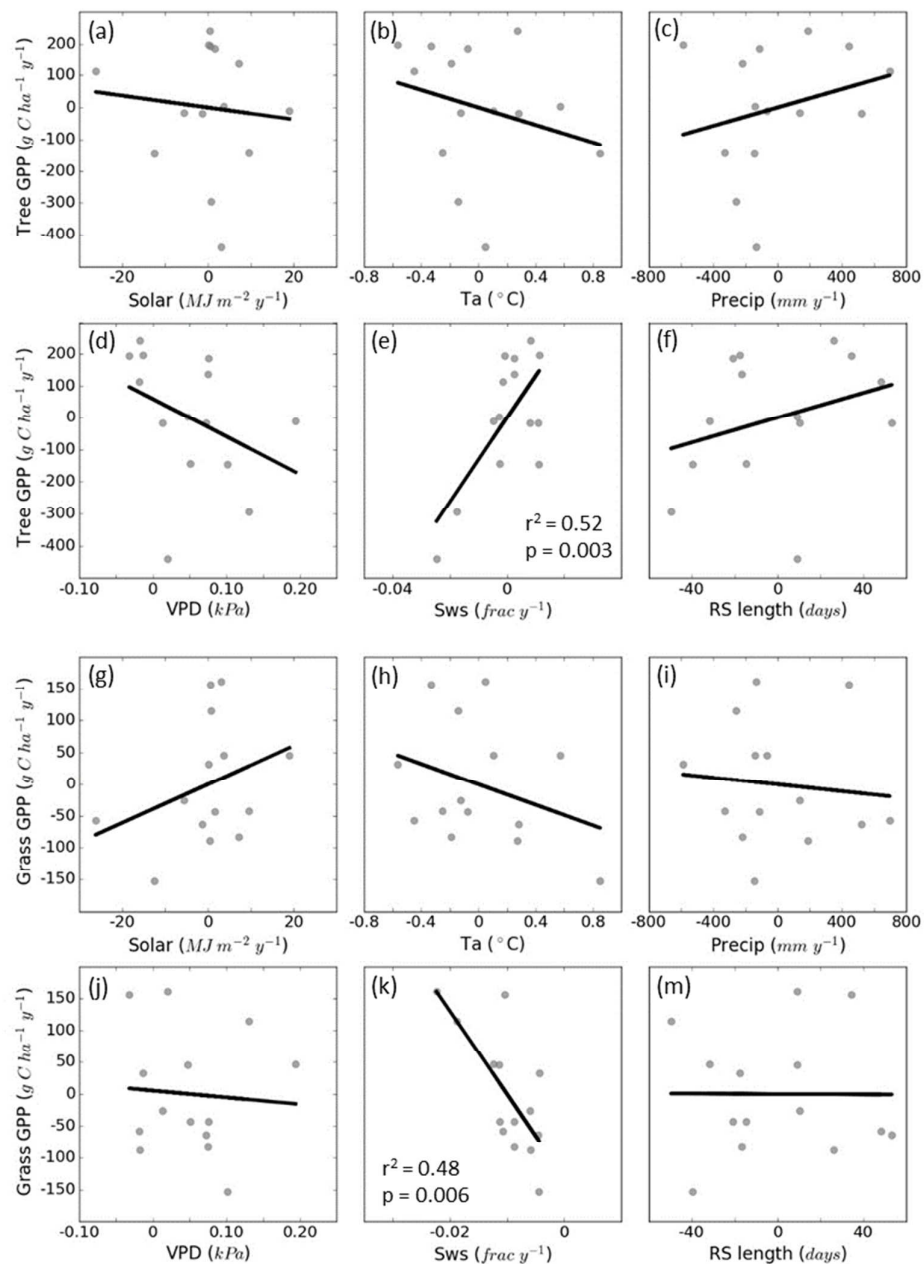


Figure 6: Linear regression relationships of yearly solar radiation (Solar, a & g), air temperature (Ta, b & h), rainfall (Precip, c & i), vapour pressure deficit (VPD, d & j), soil water storage (Sws, e & k) and rainy season (RS, f & m) length anomalies against tree and grass gross primary productivity (GPP) anomalies for the Howard Springs site from 2001 to 2015. Anomalies represent the change from the 2001-2015 mean,

based on water-years (i.e. Jul-Jun). Only significant anomaly correlations are given, as indicated on the plots by r^2 values and p values of <0.05 as a sign of statistical significant.

Variability in the tree-grass GPP ratio at Howard Springs

Under enhanced atmospheric CO₂ levels, woody thickening is likely to increase the tree-grass GPP ratio in savannas. To determine if woody thickening was occurring at Howard Springs, we calculated yearly sums of tree and grass GPP, as well as the tree-grass GPP ratio anomaly (Fig. 7). In general, over the first half of the period there was a slight increasing trend in tree GPP and a decrease in the grasses, which translated into an increase in the tree-grass GPP ratio up to 2010-2011. However, after this point, the tree-grass GPP ratio decreased (Fig. 7), with the overall result that there was no significant ($p = 0.18$) linear trend over time that would be consistent with woody thickening. As such, we cannot conclude from this dataset that woody thickening occurred at Howard Springs during this time.

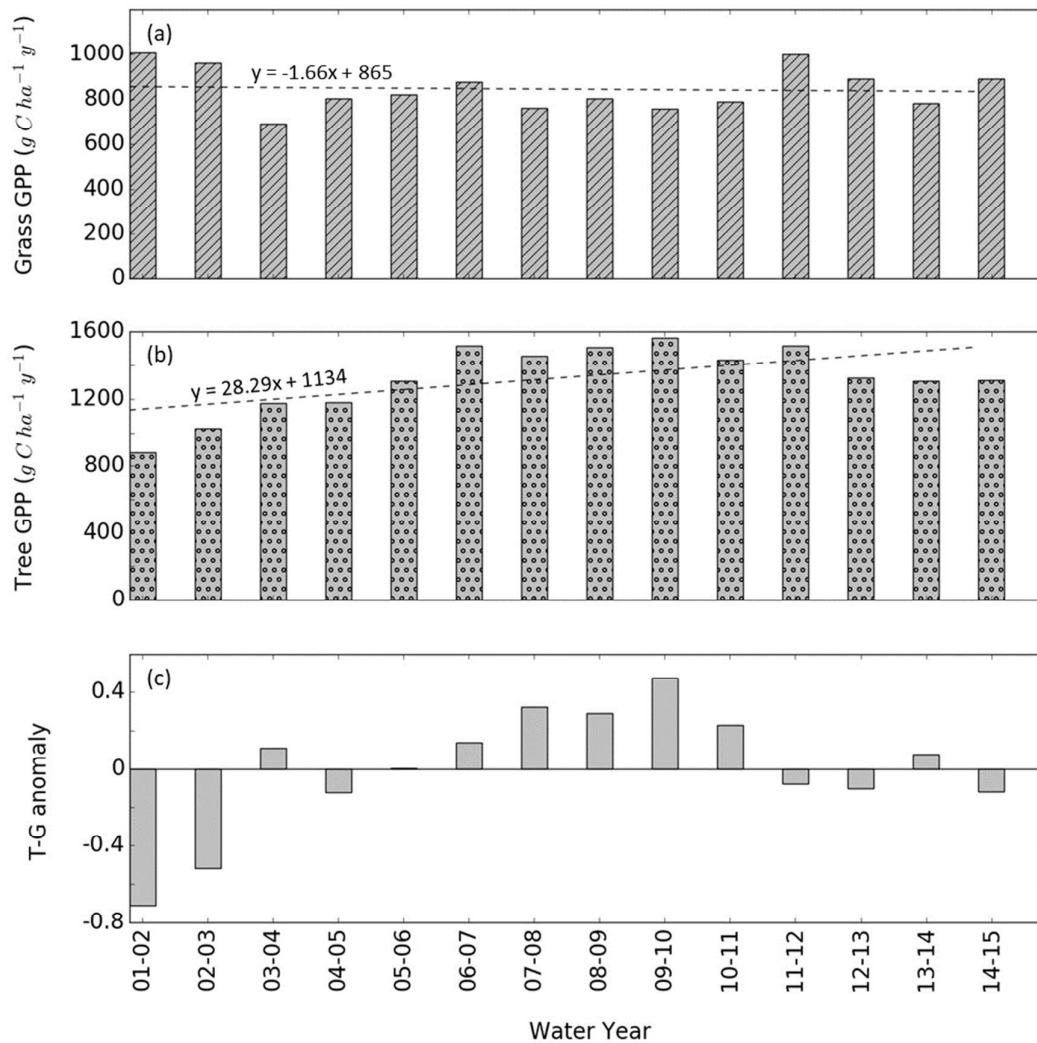


Figure 7: Annual model estimates for grass (a) and tree (b) gross primary productivity (GPP), as well as the tree-grass GPP ratio anomaly (c), for the Howard Springs savanna from the water-year (i.e. Jul-Jun) 2001-2002 to 2014-2015. Each plot also shows the trend in growth over the study period.

Despite the apparent lack of woody thickening at Howard Springs, there was still a distinct cyclical pattern in the tree-grass GPP ratio anomaly over time (Fig. 7; c) that could be

447 correlated with modes of climate variability. Recent work from Rogers & Beringer, (2016)
448 showed that IAV in rainfall for the Howard Springs region was correlated most strongly with
449 changes in the SOI, the TSI and the II. Therefore, we used these in conjunction with a
450 measure of the AUSMI to test the level of influence of the Australian monsoon on inter-
451 annual tree and grass productivity. This analysis revealed that of the four indices, the SOI had
452 a significant relationship with the tree-grass anomaly (Fig. 8) only if the level of significance
453 was relaxed to $p = 0.10$ (instead of $p = 0.05$). In general, for years when the SOI had a
454 positive value, the tree-grass anomaly was also positive, indicating a benefit to the trees over
455 the grasses. During years where the SOI was negative overall, the grasses benefited, as shown
456 by negative tree-grass anomaly values (Fig. 8).

457

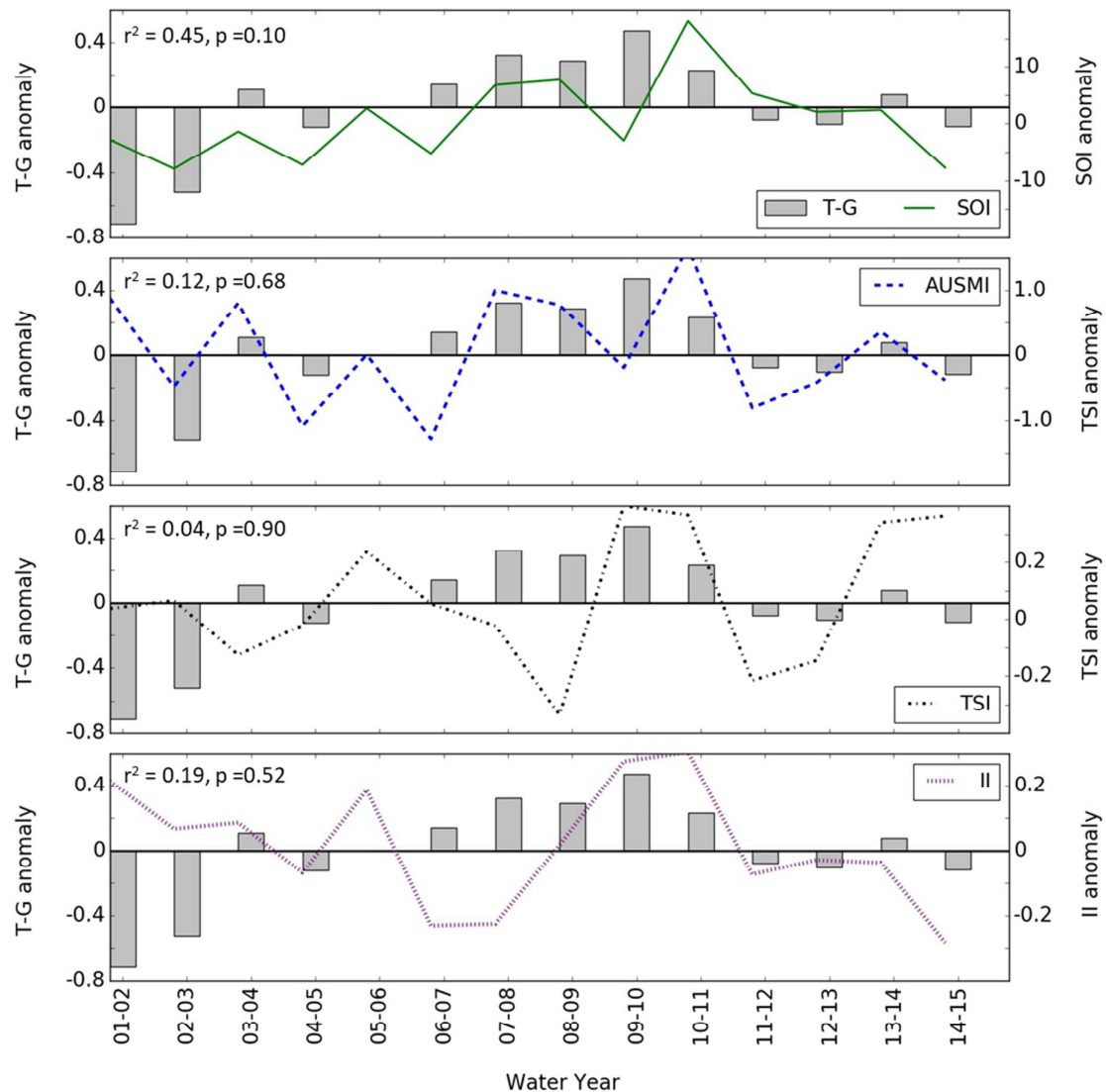


Figure 8: Time series plots of the yearly Howard Springs tree-grass anomaly against four key climate indices found to influence long-term precipitation at Howard Springs (Rogers & Beringer, 2017). These indices include the Southern Oscillation Index (SOI), the Australian Monsoon Index (AUSMI), the Tasman Sea Index (TSI) and the Indonesia Index (II). Correlation between each climate index and the tree-grass anomaly are given by the r^2 values and its level of significance is given by the p-values.

467 **Discussion**

468 We have shown how tree and grass productivity varies over the long-term in an Australian
469 tropical savanna and what the primary meteorological factors are that determine this
470 variability, both seasonally and inter-annually. Both tree and grass GPP of this savanna were
471 light limited during the wet season and water limited during the dry season. Whitley et al.,
472 (2011) concluded that mesic (high rainfall) savannas, such as Howard Springs, were light
473 limited in the wet season due to a limited capacity of the vegetation to absorb light under
474 ample soil water conditions, and in the dry season due to loss of canopy leaf area. Thick
475 cloud cover during the wet season, from the summer monsoon, can also reduce productivity
476 due to significant reductions in the quantity of total radiation (direct and diffuse) reaching the
477 land surface (Kanniah, Beringer, & Hutley, 2013). The summer monsoon is most active from
478 Dec-Mar (Cook & Heerdegen, 2001), which is when solar radiation limits tree and grass
479 productivity the most (Fig. 4). These studies highlight the complex way in which savanna
480 vegetation has adapted to its climatic range, as well as how it responds to inter-annual
481 climatic variability.

482 At the onset of the dry season the annual C₄ grasses senesce (Andrew & Mott, 1983; Moore
483 et al., 2017), leaving perennial C₄ grasses and woody understory species to contribute
484 towards GPP in the understory (Moore et al., 2016, 2017). These species rely on moisture
485 available in the surface soil layers to remain productive (Prior, Eamus, & Duff, 1997; Werner
486 & Prior, 2013) and are often dormant during the late dry season when these layers are
487 depleted (Prior et al., 2006; Werner & Prior, 2013). Likewise, the overstory tree species also
488 maximise their usage of surface soil moisture while moisture remains available in the early
489 dry season (Cook et al., 1998; Werner & Murphy, 2001). However, the trees also have an
490 extensive root system that gives them access to this deeper water during the dry season (Cook
491 et al., 1998; Eamus, Chen, Kelley, & Hutley, 2002; Kelley, O'Grady, Hutley, & Eamus, 2007;

Walker & Langridge, 1997), and they are able to maintain a nearly constant transpiration rate year-round (Hutley, O'Grady, & Eamus, 2000; O'Grady, Eamus, & Hutley, 1999). At the ecosystem scale, O'Grady, Eamus, & Hutley, (1999) found a strong coupling between tree water use and VPD, particularly during the late dry season when atmospheric VPD is at its highest, showing that the trees are limited in their ability to maintain stomatal closure. In our analysis, we found that VPD also increased slightly in importance during the late dry season (Aug-Oct) for the grasses, even though Sws at 100 cm remained the most important variable overall (Fig. 4). This result is consistent with the findings of Walker & Langridge, (1997) who concluded sub-soil moisture status has a significant influence on productivity in these savannas.

In addition to investment in deeper roots, most tree species reduce their foliage cover in order to maintain transpiration rates as soil water availability declines (Hutley, O'Grady, & Eamus, 2000; O'Grady, Eamus, & Hutley, 1999), which also reduces productivity by the late dry season (Eamus, Myers, Duff, & Williams, 1999; Prior, Eamus, & Duff, 1997). Decreasing soil water availability triggers the trees to regulate when and for how long their leaf stomata are open to reduce water loss (Eamus & Cole, 1997; Prior, Eamus, & Duff, 1997). However, as demonstrated by Myers, Williams, Fordyce, Duff, & Eamus, (1998) in an early dry season irrigation experiment, the trees can retain leaves, providing more photosynthetic structures that facilitate high rates of productivity in the dry season. The adaptive capacity of the trees to resource availability provides a likely explanation for why there was a positive correlation between increasing soil water availability and tree productivity (Fig. 6). While our analysis could be improved by the inclusion of deeper Sws monitoring (if available), we have shown the importance of soil moisture as a driver of tree-grass productivity both inter-annually and during the dry season, with increasing importance for deep soil moisture as the dry season progresses.

Another important question surrounding the future of savannas is how the tree-grass GPP ratio is likely to change as atmospheric CO₂ levels continue to increase (Scheiter & Higgins, 2009; Scheiter, Higgins, Beringer, & Hutley, 2015). While our study revealed no significant change in the tree-grass GPP ratio, a recent analysis of tree increment (i.e. from 2008 to 2014) at Howard Springs showed a biomass increase of 0.5 t C ha⁻¹ y⁻¹ (Rudge, 2015). This is at the upper end of reported tree growth for north Australian savannas (Beringer, Hutley, Tapper, & Cernusak, 2007; Cook et al., 2005; Lehmann, Prior, & Bowman, 2009; Murphy, Lehmann, Russell-Smith, & Lawes, 2014) and is consistent with reported site net ecosystem productivity (Beringer et al., 2016), site disturbance history and increasing site rainfall (Hutley & Beringer, 2010). A key finding of Rudge (2015) was that increasing biomass primarily occurred in the middle to high tree size classes and that there was little change in size class distribution (i.e. no juvenile recruitment). Therefore, woody thickening is not significant at Howard Springs. The work of Rudge (2015) shows that biomass is being accumulated at a slow rate, but that it is due to the growth of individual trees, rather than the recruitment (i.e. thickening) of saplings. This is consistent with our finding that there is no temporal trend of changing tree-grass GPP ratio over the past 15 years at Howard Springs (Figure 7; c).

Varying degrees of woody thickening have been detected at other sites in the Northern Territory savannas, including in the Kakadu (Bowman, Riley, Boggs, Lehmann, & Prior, 2008) and Litchfield (Bowman, Walsh, & Milne, 2001) national parks. Spatial variability in thickening is likely to be a long-term response to fire management in the Australian savanna region, which is highly heterogeneous (Beringer et al., 2015; Scheiter, Higgins, Beringer, & Hutley, 2015). The Howard Springs site is intensively managed each year with control burning to reduce the threat of high intensity, late dry season fires damaging the eddy covariance equipment. However, late dry season fires are a common occurrence in the

Howard Springs region (return rates of 1-3 years (Beringer et al., 2015)) as it is located approximately 5 km from a low density peri-urban development (Fig. 1; a) and receives little management from local fire authorities (Russell-Smith et al., 2013; Russell-Smith et al., 2003). These high intensity fires do encroach upon the Howard Springs flux footprint, resulting in top-kill of juveniles that would limit woody thickening (Lawes, Richards, Dathe, & Midgley, 2011; Prior et al., 2006; Prior, Williams, & Bowman, 2010) at the site. This highlights the important role fire plays in shaping savanna ecosystem structure and supports the need for further research into how it may change in the future.

Along with fire, our study revealed the importance of the SOI as a driver of tree-grass productivity at Howard Springs (Fig. 7). The SOI provides an indication of El Niño/La Niña driven climatic variability that influences T_a and F_{sd} , as well as rainfall (Broich et al., 2014; Risbey, Pook, McIntosh, Wheeler, & Hendon, 2009). As such, it has been found to correlate with vegetation productivity (Nicholls, 1986, 1991) and phenology (Broich et al., 2014) for many regions of Australia. In the northern Australian savanna region, the SOI has also been correlated with fire activity (Harris, Tapper, Packham, Orlove, & Nicholls, 2008), which is linked with grass productivity in particular.

The 15-year flux record included a record breaking La Niña year (2010-2011), which resulted in a greening pulse over much of the terrestrial southern hemisphere (Ahlström et al., 2015; Poulter et al., 2014). This greening effect was strongly evident in xeric (low rainfall) savannas of inner continental Australia (Cleverly et al., 2016), and the mesic (higher rainfall) Howard Springs savanna also experienced its highest rainfall year and lowest total solar energy year (Fig. 5). However, the response of tree and grass GPP to this anomalous year was mixed, with higher than average (but not maximum) GPP experienced by the trees and lower than average GPP experienced by the grasses (Fig. 5). However, grass GPP was at its highest in the year following the La Niña event, indicating a lag in the response of the grasses to the

rainfall surplus. Recent work from Ma, Baldocchi, Wolf, & Verfaillie, (2016) showed a similar result in an oak-grass temperate savanna in California, with the research concluding that ecosystem-level responses of tree and grass GPP were driven by slow (i.e. often lagged) responses to meteorological variability. While xeric savannas have evolved to be fast responders to climatic pulses (Cleverly et al., 2016), our results indicate that mesic savannas might be slower at responding to similar climatic pulses. As models improve at capturing savanna productivity dynamics (Whitley et al., 2017), there will be more opportunities for exploring tree-grass responses to climate across the global savanna biome.

In summary, our findings suggest that mesic and xeric savanna ecosystems might respond very differently to climate driven changes in the timing and distribution of annual rainfall and how they relate to energy availability in the wet season and soil moisture availability in the dry season. This study fills an important gap in our understanding of the long-term tree and grass productivity dynamics of a tropical savanna. By identifying the importance of light availability in the wet season and soil moisture availability in the dry season, as well as the influence of inter-annual variability in soil moisture and climate indices (i.e. SOI), it puts us one step closer towards determining how the tree-grass dynamic may shift as the climate changes in the coming century.

Author Contributions

Field work and experimental design was executed by C. Moore, J. Beringer, L. Hutley and B. Evans. Data analysis was chiefly carried out by C. Moore. The DIFFUSE model analysis was provided by R. Donohue. Code for the Random Forest analysis was provided by J. Exbrayat. The manuscript was prepared by C. Moore with contributions from all co-authors.

Data Availability

All eddy covariance data used in this study are available for download from the OzFlux website (www.ozflux.org.au), under the TERN Attribution-Share Alike- Non Commercial (TERN BY-SA-NC) Data Licence v1.0. Climate index data are available from the websites as follows: TSI and II; <http://climate-cms.unsw.wikispaces.net/ERA+INTERIM>, SOI; http://www.bom.gov.au/climate/enso/soi_monthly.txt, AUSMI; <http://apdrc.soest.hawaii.edu/projects/monsoon/ausmidx/ausmidx-djf.txt>

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For Review Only

Figure Captions

Figure 1: MODIS Land Cover Product (MCD12Q1) using the International Geosphere-Biosphere Program (IGBP) classification system for a) the Northern Territory in Australia, b) the northern-west region of the northern territory and c) the area directly surrounding the Howard Springs OzFlux tower, with individual pixel resolution of 500 m (produced in ArcMap v10.1 using MODIS Land Cover data from Gibson (2015)).

Figure 2: Time series and regression comparison of Howard Springs flux tower and DIFFUSE model estimates (Model_O = original model, Model_A = adjusted model to include understory woody contributions) of gross primary productivity (GPP, $\text{g C m}^{-2} \text{d}^{-1}$) for understory (a) and overstory (b) from September 2012 to June 2015. Regression plots show the line of best fit (solid line), the 1:1 line (dashed line), and the linear regression equation for modelled GPP (GPP_M) predicting tower GPP (GPP_T).

Figure 3: Long-term (15 year) ecosystem (Eco) gross primary productivity (GPP) flux tower time series, the partitioned overstory (O/S) and understory (U/S) GPP, plus rainfall, for the Howard Springs savanna site. Data are shown as monthly sums.

Figure 4: Meteorological drivers of monthly understory and overstory gross primary productivity (GPP) from 2001 to 2015 (a & b) and 2008 to 2015 (c & d) at Howard Springs. Meteorological drivers include soil water storage at 10 cm (Sws), Sws at 100 cm (Sws100), air temperature (T_a), vapour pressure deficit (VPD) and incoming solar radiation (Fsd). The bottom panel begins in 2008 due to the installation of the 100 cm Sws sensor in that year.

Figure 5: Anomaly plots for overstory (O/S) and understory (U/S) GPP, plus solar radiation (Solar), vapour pressure deficit (VPD), soil water storage (Sws), rainfall (Precip) and air (Ta) and soil (Ts) temperature for the Howard Springs savanna site.

Figure 6: Linear regression relationships of yearly solar radiation (Solar), air temperature (Ta) rainfall (Precip), vapour pressure deficit (VPD) soil water storage (Sws) and rainy season (RS) length anomalies against overstory (O/S) and understory (U/S) gross primary productivity (GPP) anomalies for the Howard Springs site from 2001 to 2015. Anomalies represent the change from the 2001-2015 mean, based on water-years (i.e. Jul-Jun). Correlations are given by the r^2 values, where (+) values represent a benefit of the increasing meteorological variable and (-) values represent inhibition of the increasing meteorological variable to GPP. Correlation significance is given by the p value, where p values <0.05 are significant.

Figure 7: Annual gross primary productivity (GPP) sums for the understory (U/S) and overstory (O/S), as well as the tree-grass GPP ratio anomaly, for the Howard Springs savanna from the water-year (i.e. Jul-Jun) 2001-2002 to 2014-2015. Each plot also shows the trend in growth over the study period.

Figure 8: Time series plots of the yearly Howard Springs tree-grass anomaly against four key climate indices found to influence long-term precipitation at Howard Springs (Rogers and Beringer, 2016). These indices include the Southern Oscillation Index (SOI), the Australian Monsoon Index (AUSMI), the Tasman Sea Index (TSI) and the Indonesia Index (II). Correlation between each climate index and the tree-grass anomaly are given by the r^2 values and its level of significance is given by the p-values, with p <0.05 indicating a significant relationship.

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